



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

STUDIES ON THE GEOTROPISM OF STEMS.

EDWIN BINGHAM COPELAND.

1. The absence of polarity in the hypocotyl of *Cucurbita*.

THE hypocotyl of *Cucurbita*, and, I suppose, of every plant whose cotyledons expand and act as leaves, is negatively geotropic in its ultimate reaction. When the hypocotyl is in any other position than the vertical, the under half of it grows more rapidly than the upper. This is regarded as a response to the unusual disposition of the burden of the parts of the hypocotyl, as they rest upon one another; and the seat of perceptivity and response is more specifically located in the green cortex.¹ The purpose of the reaction is to get the cotyledons into the light, which, when the seed germinates in the ground, will be accomplished by pushing them upward. Now it is evident without argument that an excess of growth of the under half of the hypocotyl will place its upper end in a vertical position, so that its further growth will be upward only in case the basal end is fixed in its position and the naturally upper end is free—a condition which is fulfilled in nature by a considerable growth of the root before the elongation of the shoot commences.

Teleologically, perhaps phylogenetically, the geotropism of the shoot has been developed along lines of "lengthwise" propriety: *i. e.*, in order to secure a particular linear arrangement of root, hypocotyl, cotyledon, etc. But in the individual plant today, according to Czapek's explanation (*loc. cit.*), which is the only rational one I am acquainted with, the response is to a disturbance of the normal "crosswise" arrangement, so that each growing part of the hypocotyl acts without reference to the parts more or less remote from the cotyledons.

The question as to whether or not any trace of the development of geotropism remains in its manifestation in the present

¹ CZAPEK, F.: Weitere Beiträge zur Kenntniss geotropischen Reizbewegungen. *Jahrb. f. wiss. Bot.* 32: 248. 1898.

plant has seemed to me worthy an experimental answer. Such a trace would appear as a sort of polarity, such that if the fixed point of the hypocotyl were moved upward from the base, only the upper free part would remain disposed to become erect. To answer this question I transferred the fixed point at once from base to apex, in each case leaving the other end free. The result was unequivocal, and as the data from several experiments were in all essentials alike, it will suffice if a single series is reported.

The seeds were germinated on a net over water and the seedlings selected were perfectly straight and as uniform as possible. The hypocotyls, 6–6.5^{cm} long, were marked off into zones of 1^{cm} each, and these zones were numbered from the cotyledons downward. The end to be fixed was imbedded in a block of gypsum plaster, and these blocks were placed, with the hypocotyl horizontal, in a closed glass vessel containing some water. The experiment was begun at 10 A.M., April 12, 1899, and at 4 P.M. the free ends were all directed upward at angles of 50–70°, those having free cotyledons being somewhat more sharply elevated than those having free roots. They were left undisturbed for six days, at a lower temperature than *Cucurbita* likes, about 18° C. in general, and were then removed and the growth and curvature measured. The curvature is expressed in the following table in figures representing the radius of the arc, measured by a Sachs' cyclometer. Plants 2 and 4 had the roots imbedded; plants 1 and 3 the cotyledons, so that zone I was next the plaster.

PLANT 1.

Hypocotyl straight and erect (the roots in air) to within 6^{mm} of the cotyledons. The radius of the curve for the upper 5^{mm} of the hypocotyl and the exposed 5^{mm} of the cotyledons was about 1^{cm}.

	Zone	I	II	III	IV	V	VI
PLANT 2.							
Curvature (in cm.)		15	9	6	3	5	15
Growth (in mm.)		3	3.5	2.7	2		
PLANT 3.							
Curvature (in cm.)		2	3	4	7	12	
Growth (in mm.)		1.7	1.2	1.3	1		
PLANT 4.							
Curvature (in cm.)		14	10	4	3	4	8
Growth (in mm.)		1.5	2	1.7	1	1	1

The conclusion, which has been anticipated, is that the response to gravity of the horizontal hypocotyl is always the same, whether the result is beneficial or, under artificial conditions, detrimental. It is a response to local conditions in each individual zone of the hypocotyl, and is executed without the slightest regard to the *relative* positions of the different zones, or the serial parts of the plant, roots, hypocotyl, cotyledons.

The pumpkin has even, figuratively, no brains. Its response to a stimulus is blind, like the instincts of animals: merely an effect, devoid in any individual instance of a purpose. As is often at least true of instinct, the response is not directly to the condition it is designed to correct, or to suit, but to something correlative, or merely concomitant. In response to a shifting of the pressure upon one another of the transverse elements of a tissue, the plant executes a change in its growth, which becomes of some service only when it results in a certain longitudinal arrangement of the plant-members; this longitudinal arrangement is the thing at fault, but the plant cannot perceive it. In nature the response meets the hidden purpose, but under changed conditions the same response is made, and is fatal. Certain flies flock at the scent of carrion, not in reality to gratify their peculiar æsthetic sense, nor yet to get a meal, but because it takes them where their eggs will thrive; the *Dictyophora* panders to their instincts; the carrion flies revel in its slime, and, mistaking the attribute for the reality, deposit their eggs where they rot. The behavior of the pumpkin and the fly is essentially the same; both react blindly, but in nature, fortunately.

A careful inspection of the table given above will show, in the different location of the region of greatest curvature in the plants with encased roots and in those with encased cotyledons, a nice demonstration that each zone of the hypocotyl can act for itself. In the former the hypocotyl is somewhat curved throughout, even in the most mature basal part, and most so about 4^{cm} below the cotyledons, the upper, youngest part being almost straight; while when the cotyledons were encased the curvature

is most marked within 1^{cm} of them, and the older part is straight. This difference could not occur if each zone were not able both to be geotropically irritated, and to respond to the irritation. If the experiments lasted several days it was found that the stems which were fixed at the apex were usually more curved than those fixed normally, at the base, so that in this case the end in the air was carried well beyond the vertical position. This was obviously because the youngest part remained horizontal, and as the older part matured with more or less curve the part still growing kept bending itself upright, and so carried the older part beyond the vertical.

The hypocotyls of *Helianthus annuus* and *Lupinus albus* and the epicotyls of *Pisum sativum* and *Phaseolus vulgaris* were tested, but showed no behavior different from that of *Cucurbita*, so that it is not worth while to encumber this paper with the individual results. The nutation of *Phaseolus* caused some queer curves, and the same would probably be found the case with *Cucurbita* when the epicotyl changes from orthotropic to plagiotropic. The behavior in response to stimulation by light is analogous. No experiments were undertaken especially to show this; but when seeds of *Lupinus* were germinated in holes in a floating cork in a glass vessel, and grew so that the cotyledons kept their place while the hypocotyls extended downward into the water, the latter became concave on the light side, and the roots were carried toward the window.

Any indication of real polarity is likewise wanting in roots. This is not easily demonstrated, as the curvature is largely executed in the roots of the plants I have been using, within 1.5–2^{mm} of the tip, and it is difficult to imbed them so that the tip will stay fast without encasing the part which should be free to react. Nevertheless, I have succeeded occasionally with the roots of *Cucurbita*, *Lupinus*, *Helianthus*, and *Pisum*, and in every case the result was an excess of growth of the upper side of the root, by which the shoot end of the plant was carried downward. This went as far as about 90°, but I have hitherto been unable to make the tip stay imbedded while the free end is bent

around indefinitely, as F. Darwin² did with the cotyledons of *Sorghum*.

2. The geotropism of split stems.

While it is certain that every growing part of the stem can perceive the geotropic stimulus and execute the response *in loco* it is not impossible that if the local perceptivity could be interfered with, a growing zone might respond to a stimulus transmitted to it from another part of the plant. My first experiments with split hypocotyls were with a view to answering the question; but they were not appropriate, because, as Sachs³ showed, and as anybody can easily demonstrate, a half stem is in itself irritable. The results which they did yield, however, were surprising enough.

Cucurbita.—The first experiments were on *Cucurbita* hypocotyls, partly or wholly split, the split being either transverse or parallel to the plane of the cotyledons. Of three similar experiments it will suffice to report the following one, which began May 24, and lasted forty-eight hours. The growth is reported, and the angle made by the free end with its original horizontal position.

			Growth in mm	Curva- ture in degrees				Growth in mm	Curva- ture in degrees
1	Free	-	40	80	5	Split horizontal	-	18	180
2	Split vertical	-	8	75	6	Split horizontal	-	10	165
3	Split vertical	-	4	70	7	Split horizontal	-	5	180
4	Split horizontal	-	13	110					

No. 1 was fastened in place without imbedding; nos. 5 and 6 had the cotyledons imbedded; and the others, the roots. The

²F. DARWIN, in "Botany at the British Association," *Nature* 61: 67. Nov. 16. 1899. After other evidence that geotropic perceptivity is localized in the cotyledon while the hypocotyl executes the response, he says: "If the seedling is supported by its cotyledon (which is fixed in a horizontal position) while the hypocotyl projects freely . . . the hypocotyl begins to curve upward . . . and it does not cease to curve when the free end points vertically upward; the curvature continues indefinitely, so that the hypocotyl curls into a spiral of three or four rings."

³SACHS: *Ueber Wachsthum und Geotropismus aufrechter Stengel*. *Gesammelte Abhandlungen* 2: 969. 1893. In the experiment Sachs reports, the growth of the lower half did not overcome the tissue tensions.

depressed growth of nos. 2 and 7 is correlative with the imbedding, as well as due to the wound. Removing the plumule does not hinder the elongation of the hypocotyl. When the split was horizontal the halves became bowed apart, and the angle of curvature given is the least at which they could be brought into continuous contact.

The first notion suggested by the excessive curvature of the hypocotyls with horizontal split surface is that they are responding to a stimulus received by the imbedded part of the plant. But the facts that a half stem is known to be in itself irritable, and that the extreme curvature, 180° , occurred whether it was root or cotyledon that remained horizontal, point toward the conclusion that in the experiment each half of the split hypocotyl responds only to a stimulus received *in loco*; and that a half hypocotyl has something in its own structure, independent of any comparison of conditions with the other half, which will make it grow more rapidly if the split is the upper than if it is the lower surface.

Two plants were next split from the tops well into the roots, one having the cotyledons split, the other separated; both had the roots imbedded. The halves of one were too weak to become quite erect, but those of the other bent up side by side, and after they became erect the lower half slid along the upper so as to reach beyond it. In both cases the growth of the lower half exceeded that of the upper by 3^{mm} . The experiment was repeated, giving a little less difference.

July 13, a number of plants were split from end to end, and the entirely separated halves imbedded side by side, some with the roots, others with the cotyledons free, all with the cut surface horizontal. The growth in forty-eight hours follows:

						Growth of upper half in mm	Growth of lower half in mm
1.	-	-	-	-	-	2.5	3.5
2.	-	-	-	-	-	2.0	3.5
3.	-	-	-	-	-	2.5	4.0
4.	-	-	-	-	-	3.5	5.0
5.	-	-	-	-	-	2.0	2.3
6.	-	-	-	-	-	3.0	4.0

In every instance the lower half grew more than the upper.

July 14 the experiment was repeated with older plants. The average growth of nine plants in forty-eight hours was: in the upper half, 1.5^{mm} ; in the lower half, 2.2^{mm} . In every instance except one the greater growth was made by the lower half. It occasionally chanced that one half twisted into the other's position, which caused the difference to be wanting or less marked.

Later in the year in connection with work on other plants, I put five split plants into glass tubes too small to let them bend. The average growth of the lower halves in three days was 26^{mm} ; of the upper halves, 16^{mm} . At the same time I made a small attempt to see what is the rate of growth of a horizontal half stem in either position as compared to one in its natural erect position. Three plants were split throughout, and one half of each was put into an upright glass tube. In three days the average growth was 4.8^{mm} . The other halves were put into horizontal tubes, with their split surfaces up, and grew in the same time on an average 14.3^{mm} . Of three other plants the average growth of the erect halves was 24^{mm} , and of the horizontal halves with split surface down, 24.3^{mm} ; but two of these latter had twisted so that part of their growth was made with the cut surface up. The comparative growth of erect and horizontal halves was more fully experimented on with *Lupinus*.

Phaseolus vulgaris. Three epicotyls, $4-5^{\text{mm}}$ in length, were split November 3, and the cotyledons were imbedded so that the split surfaces were horizontal. In three days the average growth of the upper halves was 3.2^{mm} ; of the lower, 5.7^{mm} . The curves necessary to bring the halves together were $95-145^{\circ}$. November 20, six epicotyls were split, and the halves fastened in the same positions with glass needles. In two days the average growth of the upper halves was 25^{mm} ; of the lower, 27.2^{mm} . Small as the average difference is, the lower half was longer in every instance.

Caladium sp. On large corms that had been brought into the greenhouse for the winter the stubs of the shoots were still growing slowly. These stubs were made up of some very young

leaves in the middle, surrounded by the fleshy petioles of the leaves the rest of which had been removed. Two of these petiole stubs were present, each reaching around far enough so that its edges lapped over one another. These petioles should execute any curving that occurs. I cut the end of the stub off square, and then split it into several slices, in such a plane that the upper and lower parts of the larger outer cotyledon were symmetrical, and placed the corms so that the split surfaces were horizontal. The atmosphere was unfortunately not saturated, and cutting and splitting the fleshy parenchyma gave such an opportunity for evaporation that in most cases after a week a shortening instead of an elongation had occurred. Nevertheless, a slight upward curve of each slice was noticeable, and a difference in their growth could be detected in spite of the shrinking. The following two experiments may represent the five made:

1. Diameter of stub, 3mm. Cut into four equally thick slices. Change in length of outer petiole in six days :			2. Diameter 35mm : in five slices. Change in six days :	
1st (undermost) slice.	no change		1st (undermost) slice.	+1 mm
2d	"	—1 mm	2d	—0.4mm
3d	"	—1.3mm	3d	—0.6mm
4th	"	—2 mm	4th	—1.0mm
			5th	—2.0mm

It appears then that where these composite stem structures are split into a series of slices the growth of these is successively less from below upward. Some of these slices consisted (aside from the epidermis) entirely of the large celled cortical parenchyma, and seemed able individually to execute geotropic curvatures. *Caladium* is the only subject with which I have succeeded in getting a series of longitudinal slices of sufficiently equal thickness to give any kind of results.

Helianthus. Nine hypocotyls of the "mammoth Russian" variety were split, the cotyledons being either separated or split, and the split extending 1^{cm} into the root. They were placed in horizontal glass tubes. After a day, four plants in which the difference in the growth of the halves was well marked were turned over, so that the halves exchanged places.

	December 5. Length in mm.	December 6. Growth in mm.		December 8—Growth from December 5. in mm.	
		Lower half.	Upper half.	Former lower half.	Former upper half.
1.	17	6	3	8	6
2.	30	8	5	15	26
3.	27	8	6	13	26
4.	25	8	4	16	15
5.	26	8.5	5		
6.	13	9	8		
7.	26	6	5		
8.	15	6	5		
9.	35	18	16		

The average growth of the under halves of the first four during the first day was 7.5^{mm} : during the following two days, when they were the upper halves, their average was only 5.5^{mm} . The average of the upper halves changed at the same time from 4.5^{mm} to 13.75^{mm} . There is no possibility of error either from unequal splitting or individual variability in these results.

Lupinus albus. The large, straight, solid hypocotyls of *Lupinus* are the finest subjects I have found for these experiments, and have been very freely used. November 15 four plants were split throughout, and imbedded at either end. After three days the average growth of the upper halves was 4.25^{mm} ; of the lower halves, 10.5^{mm} . The lower half was always the more curved, in spite of the tissue tensions which at first bent it downward. It was indifferent whether the cotyledons were split or separated. Of a number of plants started November 17, and marked into 1^{cm} zones, the following two were interesting in their behavior. Both twisted so that the halves changed positions. After three days the growth of each half of one of them was 14^{mm} : at first the lower half gained (as was shown by measuring the individual zones), and then after their positions were reversed the other caught up. The upper and lower halves of the other plant grew respectively 15^{mm} and 13^{mm} , but before they changed places the lower was 2^{mm} ahead. Of six plants split and put into glass tubes, November 28, so that they might grow in length but could not curve, the average excess in length of the lower half after two days was 5^{mm} . Of seven plants

treated in the same way December 1, the average growth of the upper half in two days was 4.4^{mm}; of the lower, 9.1^{mm}. Of thirteen plants split 1^{cm} into the root and placed in horizontal tubing, the average growth of the upper halves in two days was 2.4^{mm}, and of the lower halves, 4.4^{mm}. Three plants were turned over; and after two more days the halves of two of them were equal, but in the other the difference had increased.

It has now been shown for hypocotyls and epicotyls, hollow and solid stems, fixed at either end by imbedding in gypsum plaster or pinning with glass pins, or grown in glass tubes, that the rate of growth of an isolated half stem is greater, in general perhaps twice as great, if it occupies the position of the inferior half of an uninjured prostrate stem, than if it is in the position of the superior half. As to the fact, the proof is surely sufficient. But so far no explanation has suggested itself, which was not more easily confuted than conceived.

After looking in vain for a real reason, I turned to the mechanism of the growth, but have been unable in a considerable number of experiments to detect any well marked or constant difference in turgor between the halves. If the turgor of the growing region at a fixed distance below the insertion of the cotyledons is determined it will be found less in the upper half, but this is because the growing region is shortened. If the zone which is elongating most rapidly is tested in each case (this will be perhaps 2^{mm} nearer the base in the under half) there will be found almost no difference in the turgor. The results from testing a number of plants were very constant, and the following may serve as an example. The halves had been horizontal for four days. Turgor is measured in percentage concentration of KNO₃ necessary to begin plasmolysis.

Lupinus albus.

Growth	Upper half 7 ^{mm}		Lower half 15 ^{mm}	
	Growing part	Grown part	Growing part	Grown part
Turgor { Pith	- 4	3	4	3.5
{ Cortex	4	3-3.5	4	3-3.5

Ceteris paribus, however, the more rapid growth of the lower half would depress its turgor,⁴ so that the equality observed indicates that with equal growth the lower half would have its turgor raised. It was noticeable that in general the relation of turgor in pith and cortex was the same in both halves (as in the growing part, in the figures just given); although to bring a pressure to bear against the tube which kept them straight, one half should manifest an excess of turgor in the cortex, the other rather in the pith. I do not know whether or not the entire stems would show any difference in the turgor of the halves, such as Pfeffer⁵ observed in some grass nodes; but they do exert an upward pressure by the elimination by growth of the tension between the walls and cell-sap of the under side, so that the osmotic pressure is available for outside work. If a hypocotyl of *Lupinus* be removed from a horizontal glass tube and immediately split, the lower half stretches out, often at least 2^{mm} longer than the upper, and this difference is maintained after entire plasmolysis.

To determine the effect of the position of the horizontal half-stems on the rate of growth, as compared with the normal upright position, I paired a number of plants, split them, matched the halves of each plant with those of the other plant of the same pair, put them into glass tubes, and placed one tube erect, the other horizontal. Then one half of *A* and one half of *B* were erect; the other half of *A* was horizontal with the split surface up, and the other half of *B* was horizontal with the split surface down. They were wrapped in moist filter paper, and except for their position with regard to gravity were under as like conditions as could be desired. Of a series of six plants treated in this way, the growth of the erect halves in two days averaged 7^{mm}. The growth of the horizontal halves, whose cut surface was downward averaged 6.8^{mm}. At the same time the complementary six plants averaged: the erect halves, 8.1^{mm}, and the horizontal halves, with split surface up, 17.1^{mm}. Dec. 8, ten

⁴COPELAND: Ueber den Einfluss von Licht und Temperatur auf den Turgor. Inaug.-Diss. Halle a. S. 1896.

⁵PFEFFER: Druck und Arbeitsleistung durch wachsende Pflanzen.

pairs of plants were treated in the same manner. In three days the average growth was :

Of ten erect halves	-	-	-	-	-	-	-	15.7 ^{mm}
Of corresponding horizontal halves, split surface down	-	-	-	-	-	-	-	13.9 ^{mm}
Of other ten erect halves	-	-	-	-	-	-	-	12.8 ^{mm}
Of horizontal halves, split surface up	-	-	-	-	-	-	-	22.9 ^{mm}

Or, calling the growth of the erect halves 100, that of the horizontal halves with split down was 88.5 ; that of horizontal halves with split up, 178.9.

The growth of the isolated under half then is decidedly accelerated, while that of the upper half is in a lesser measure retarded. Sachs⁶ long ago showed that this happens when an entire stem executes its response to geotropism, and it is interesting to note that isolation of the halves does not affect the quality of the reaction at all. This ought to give the quietus to all of the various theories which would explain the execution of the geotropic response by processes taking place entirely in either half.

The behavior of split stems emphasizes the fact that geotropic irritability is dependent upon the relative positions of the tissues of the stem : and seems to me to point toward a more intimate connection of the perception of the stimulus with the execution of the response than we have hitherto felt justified in assuming. The execution of the response by whole stems does not demonstrate any transverse transmission of a stimulus by which the halves compare their positions, for the behavior of the separate halves shows that no comparison is required.

UNIVERSITY OF WEST VIRGINIA,
Morgantown.

⁶SACHS: Längenwachsthum der Ober- und Unterseite horizontal gelegter sich aufwärts krummender Sprosse. Gesammelte Abhandlungen 2: 945. (From Arb. des botan. Inst. zu Würzburg 1: 193. 1872). On p. 955 he says: "Bei der Aufwärtskrümmung eines frei horizontal gelegten Sprosses wächst von je zwei gleichnamigen Gewebestreifen immer der der unteren, konvexen Seite stärker, der der oberen, konkaven Seite schwächer als die gleichnamigen Gewebestreifen eines aufrechten Sprosses in derselben Zeit."